

opment is today a conscious, highly specialized effort carried out by professional scientists. They already know about the hundreds of existing crops and set out to develop yet another one. To achieve that goal, they plant many different seeds or roots, select the best progeny and plant their seeds, apply knowledge of genetics to develop good varieties that breed true, and perhaps even use the latest techniques of genetic engineering to transfer specific useful genes. At the Davis campus of the University of California, an entire department (the Department of Pomology) is devoted to apples and another (the Department of Viticulture and Enology) to grapes and wine.

But plant domestication goes back over 10,000 years. Early farmers surely didn't use molecular genetic techniques to arrive at their results. The first farmers didn't even have any existing crop as a model to inspire them to develop new ones. Hence they couldn't have known that, whatever they were doing, they would enjoy a tasty treat as a result.

How, then, did early farmers domesticate plants unwittingly? For example, how did they turn poisonous almonds into safe ones without knowing what they were doing? What changes did they actually make in wild plants, besides rendering some of them bigger or less poisonous? Even for valuable crops, the times of domestication vary greatly: for instance, peas were domesticated by 8000 B.C., olives around 4000 B.C., strawberries not until the Middle Ages, and pecans not until 1846. Many valuable wild plants yielding food prized by millions of people, such as oaks sought for their edible acorns in many parts of the world, remain untamed even today. What made some plants so much easier or more inviting to domesticate than others? Why did olive trees yield to Stone Age farmers, whereas oak trees continue to defeat our brightest agronomists?

LET'S BEGIN BY looking at domestication from the plant's point of view. As far as plants are concerned, we're just one of thousands of animal species that unconsciously "domesticate" plants.

Like all animal species (including humans), plants must spread their offspring to areas where they can thrive and pass on their parents' genes. Young animals disperse by walking or flying, but plants don't have that option, so they must somehow hitchhike. While some plant species have seeds adapted for being carried by the wind or for floating on water, many

CHAPTER 7

HOW TO MAKE AN ALMOND

IF YOU'RE A HIKER WHOSE APPETITE IS JADED BY FARM-grown foods, it's fun to try eating wild foods. You know that some wild plants, such as wild strawberries and blueberries, are both tasty and safe to eat. They're sufficiently similar to familiar crops that you can easily recognize the wild berries, even though they're much smaller than those we grow. Adventurous hikers cautiously eat mushrooms, aware that many species can kill us. But not even ardent nut lovers eat wild almonds, of which a few dozen contain enough cyanide (the poison used in Nazi gas chambers) to kill us. The forest is full of many other plants deemed inedible.

Yet all crops arose from wild plant species. How did certain wild plants get turned into crops? That question is especially puzzling in regard to the many crops (like almonds) whose wild progenitors are lethal or bad-tasting, and to other crops (like corn) that look drastically different from their wild ancestors. What cavewoman or caveman ever got the idea of "domesticating" a plant, and how was it accomplished?

Plant domestication may be defined as growing a plant and thereby, consciously or unconsciously, causing it to change genetically from its wild ancestor in ways making it more useful to human consumers. Crop devel-

others trick an animal into carrying their seeds, by wrapping the seed in a tasty fruit and advertising the fruit's ripeness by its color or smell. The hungry animal plucks and swallows the fruit, walks or flies off, and then spits out or defecates the seed somewhere far from its parent tree. Seeds can in this manner be carried for thousands of miles.

It may come as a surprise to learn that plant seeds can resist digestion by your gut and nonetheless germinate out of your feces. But any adventurous readers who are not too squeamish can make the test and prove it for themselves. The seeds of many wild plant species actually *must* pass through an animal's gut before they can germinate. For instance, one African melon species is so well adapted to being eaten by a hyena-like animal called the aardvark that most melons of that species grow on the latrine sites of aardvarks.

As an example of how would-be plant hitchhikers attract animals, consider wild strawberries. When strawberry seeds are still young and not yet ready to be planted, the surrounding fruit is green, sour, and hard. When the seeds finally mature, the berries turn red, sweet, and tender. The change in the berries' color serves as a signal attracting birds like thrushes to pluck the berries and fly off, eventually to spit out or defecate the seeds.

Naturally, strawberry plants didn't set out with a conscious intent of attracting birds when, and only when, their seeds were ready to be dispersed. Neither did thrushes set out with the intent of domesticating strawberries. Instead, strawberry plants evolved through natural selection. The greener and more sour the young strawberry, the fewer the birds that destroyed the seeds by eating berries before the seeds were ready; the sweeter and redder the final strawberry, the more numerous the birds that dispersed its ripe seeds.

Countless other plants have fruits adapted to being eaten and dispersed by particular species of animals. Just as strawberries are adapted to birds, so acorns are adapted to squirrels, mangos to bats, and some sedges to ants. That fulfills part of our definition of plant domestication, as the genetic modification of an ancestral plant in ways that make it more useful to consumers. But no one would seriously describe this evolutionary process as domestication, because birds and bats and other animal consumers don't fulfill the other part of the definition: they don't consciously grow plants. In the same way, the early unconscious stages of crop evolution from wild plants consisted of plants evolving in ways that attracted humans to eat and disperse their fruit without yet intentionally growing

them. Human latrines, like those of aardvarks, may have been a testing ground of the first unconscious crop breeders.

LATRINES ARE MERELY one of the many places where we accidentally sow the seeds of wild plants that we eat. When we gather edible wild plants and bring them home, some spill en route or at our houses. Some fruit rots while still containing perfectly good seeds, and gets thrown out uneaten into the garbage. As parts of the fruit that we actually take into our mouths, strawberry seeds are tiny and inevitably swallowed and defecated, but other seeds are large enough to be spat out. Thus, our spittoons and garbage dumps joined our latrines to form the first agricultural research laboratories.

At whichever such "lab" the seeds ended up, they tended to come from only certain individuals of edible plants—namely, those that we preferred to eat for one reason or another. From your berry-picking days, you know that you select particular berries or berry bushes. Eventually, when the first farmers began to sow seeds deliberately, they would inevitably sow those from the plants they had chosen to gather, even though they didn't understand the genetic principle that big berries have seeds likely to grow into bushes yielding more big berries.

So, when you wade into a thorny thicket amid the mosquitoes on a hot, humid day, you don't do it for just any strawberry bush. Even if unconsciously, you decide which bush looks most promising, and whether it's worth it at all. What are your unconscious criteria?

One criterion, of course, is size. You prefer large berries, because it's not worth your while to get sunburned and mosquito bitten for some lousy little berries. That provides part of the explanation why many crop plants have much bigger fruits than their wild ancestors do. It's especially familiar to us that supermarket strawberries and blueberries are gigantic compared with wild ones; those differences arose only in recent centuries.

Such size differences in other plants go back to the very beginnings of agriculture, when cultivated peas evolved through human selection to be 10 times heavier than wild peas. The little wild peas had been collected by hunter-gatherers for thousands of years, just as we collect little wild blueberries today, before the preferential harvesting and planting of the most appealing largest wild peas—that is, what we call farming—began automatically to contribute to increases in average pea size from genera-

tion to generation. Similarly, supermarket apples are typically around three inches in diameter, wild apples only one inch. The oldest corn cobs are barely more than half an inch long, but Mexican Indian farmers of A.D. 1500 already had developed six-inch cobs, and some modern cobs are one and a half feet long.

Another obvious difference between seeds that we grow and many of their wild ancestors is in bitterness. Many wild seeds evolved to be bitter, bad-tasting, or actually poisonous, in order to deter animals from eating them. Thus, natural selection acts oppositely on seeds and on fruits. Plants whose fruits are tasty get their seeds dispersed by animals, but the seed itself within the fruit has to be bad-tasting. Otherwise, the animal would also chew up the seed, and it couldn't sprout.

Almonds provide a striking example of bitter seeds and their change under domestication. Most wild almond seeds contain an intensely bitter chemical called amygdalin, which (as was already mentioned) breaks down to yield the poison cyanide. A snack of wild almonds can kill a person foolish enough to ignore the warning of the bitter taste. Since the first stage in unconscious domestication involves gathering seeds to eat, how on earth did domestication of wild almonds ever reach that first stage?

The explanation is that occasional individual almond trees have a mutation in a single gene that prevents them from synthesizing the bitter-tasting amygdalin. Such trees die out in the wild without leaving any progeny, because birds discover and eat all their seeds. But curious or hungry children of early farmers, nibbling wild plants around them, would eventually have sampled and noticed those nonbitter almond trees. (In the same way, European peasants today still recognize and appreciate occasional individual oak trees whose acorns are sweet rather than bitter.) Those nonbitter almond seeds are the only ones that ancient farmers would have planted, at first unintentionally in their garbage heaps and later intentionally in their orchards.

Already by 8000 B.C. wild almonds show up in excavated archaeological sites in Greece. By 3000 B.C. they were being domesticated in lands of the eastern Mediterranean. When the Egyptian king Tutankhamen died, around 1325 B.C., almonds were one of the foods left in his famous tomb to nourish him in the afterlife. Lima beans, watermelons, potatoes, eggplants, and cabbages are among the many other familiar crops whose wild ancestors were bitter or poisonous, and of which occasional sweet individ-

uals must have sprouted around the latrines of ancient hikers.

While size and tastiness are the most obvious criteria by which hunter-gatherers select wild plants, other criteria include fleshy or seedless fruits, oily seeds, and long fibers. Wild squashes and pumpkins have little or no fruit around their seeds, but the preferences of early farmers selected for squashes and pumpkins consisting of far more flesh than seeds. Cultivated bananas were selected long ago to be all flesh and no seed, thereby inspiring modern agricultural scientists to develop seedless oranges, grapes, and watermelons as well. Seedlessness provides a good example of how human selection can completely reverse the original evolved function of a wild fruit, which in nature serves as a vehicle for dispersing seeds.

In ancient times many plants were similarly selected for oily fruits or seeds. Among the earliest fruit trees domesticated in the Mediterranean world were olives, cultivated since around 4000 B.C. for their oil. Crop olives are not only bigger but also oilier than wild ones. Ancient farmers selected sesame, mustard, poppies, and flax as well for oily seeds, while modern plant scientists have done the same for sunflower, safflower, and cotton.

Before that recent development of cotton for oil, it was of course selected for its fibers, used to weave textiles. The fibers (termed lint) are hairs on the cotton seeds, and early farmers of both the Americas and the Old World independently selected different species of cotton for long lint. In flax and hemp, two other plants grown to supply the textiles of antiquity, the fibers come instead from the stem, and plants were selected for long, straight stems. While we think of most crops as being grown for food, flax is one of our oldest crops (domesticated by around 7000 B.C.). It furnished linen, which remained the chief textile of Europe until it became supplanted by cotton and synthetics after the Industrial Revolution.

SO FAR, ALL the changes that I've described in the evolution of wild plants into crops involve characters that early farmers could actually notice—such as fruit size, bitterness, fleshiness, and oiliness, and fiber length. By harvesting those individual wild plants possessing these desirable qualities to an exceptional degree, ancient peoples unconsciously dispersed the plants and set them on the road to domestication.

In addition, though, there were at least four other major types of change that did not involve berry pickers making visible choices. In these cases the

berry pickers caused changes either by harvesting available plants while other plants remained unavailable for invisible reasons, or by changing the selective conditions acting on plants.

The first such change affected wild mechanisms for the dispersal of seeds. Many plants have specialized mechanisms that scatter seeds (and thereby prevent humans from gathering them efficiently). Only mutant seeds lacking those mechanisms would have been harvested and would thus have become the progenitors of crops.

A clear example involves peas, whose seeds (the peas we eat) come enclosed in a pod. Wild peas have to get out of the pod if they are to germinate. To achieve that result, pea plants evolved a gene that makes the pod explode, shooting out the peas onto the ground. Pods of occasional mutant peas don't explode. In the wild the mutant peas would die entombed in their pod on their parent plants, and only the popping pods would pass on their genes. But, conversely, the only pods available to humans to harvest would be the nonpopping ones left on the plant. Thus, once humans began bringing wild peas home to eat, there was immediate selection for that single-gene mutant. Similar nonpopping mutants were selected in lentils, flax, and poppies.

Instead of being enclosed in a poppable pod, wild wheat and barley seeds grow at the top of a stalk that spontaneously shatters, dropping the seeds to the ground where they can germinate. A single-gene mutation prevents the stalks from shattering. In the wild that mutation would be lethal to the plant, since the seeds would remain suspended in the air, unable to germinate and take root. But those mutant seeds would have been the ones waiting conveniently on the stalk to be harvested and brought home by humans. When humans then planted those harvested mutant seeds, any mutant seeds among the progeny again became available to the farmers to harvest and sow, while normal seeds among the progeny fell to the ground and became unavailable. Thus, human farmers reversed the direction of natural selection by 180 degrees: the formerly successful gene suddenly became lethal, and the lethal mutant became successful. Over 10,000 years ago, that unconscious selection for nonshattering wheat and barley stalks was apparently the first major human "improvement" in any plant. That change marked the beginning of agriculture in the Fertile Crescent.

The second type of change was even less visible to ancient hikers. For annual plants growing in an area with a very unpredictable climate, it

could be lethal if all the seeds sprouted quickly and simultaneously. Were that to happen, the seedlings might all be killed by a single drought or frost, leaving no seeds to propagate the species. Hence many annual plants have evolved to hedge their bets by means of germination inhibitors, which make seeds initially dormant and spread out their germination over several years. In that way, even if most seedlings are killed by a bout of bad weather, some seeds will be left to germinate later.

A common bet-hedging adaptation by which wild plants achieve that result is to enclose their seeds in a thick coat or armor. The many wild plants with such adaptations include wheat, barley, peas, flax, and sunflowers. While such late-sprouting seeds still have the opportunity to germinate in the wild, consider what must have happened as farming developed. Early farmers would have discovered by trial and error that they could obtain higher yields by tilling and watering the soil and then sowing seeds. When that happened, seeds that immediately sprouted grew into plants whose seeds were harvested and planted in the next year. But many of the wild seeds did not immediately sprout, and they yielded no harvest.

Occasional mutant individuals among wild plants lacked thick seed coats or other inhibitors of germination. All such mutants promptly sprouted and yielded harvested mutant seeds. Early farmers wouldn't have noticed the difference, in the way that they did notice and selectively harvest big berries. But the cycle of sow / grow / harvest / sow would have selected immediately and unconsciously for the mutants. Like the changes in seed dispersal, these changes in germination inhibition characterize wheat, barley, peas, and many other crops compared with their wild ancestors.

The remaining major type of change invisible to early farmers involved plant reproduction. A general problem in crop development is that occasional mutant plant individuals are more useful to humans (for example, because of bigger or less bitter seeds) than are normal individuals. If those desirable mutants proceeded to interbreed with normal plants, the mutation would immediately be diluted or lost. Under what circumstances would it remain preserved for early farmers?

For plants that reproduce themselves, the mutant would automatically be preserved. That's true of plants that reproduce vegetatively (from a tuber or root of the parent plant), or that are hermaphrodites capable of fertilizing themselves. But the vast majority of wild plants don't reproduce

that way. They're either hermaphrodites incapable of fertilizing themselves and forced to interbreed with other hermaphrodite individuals (my male part fertilizes your female part, your male part fertilizes my female part), or else they occur as separate male and female individuals, like all normal mammals. The former plants are termed self-incompatible hermaphrodites; the latter, dioecious species. Both were bad news for ancient farmers, who would thereby have promptly lost any favorable mutants without understanding why.

The solution involved another type of invisible change. Numerous plant mutations affect the reproductive system itself. Some mutant individuals developed fruit without even having to be pollinated, resulting in our seedless bananas, grapes, oranges, and pineapples. Some mutant hermaphrodites lost their self-incompatibility and became able to fertilize themselves—a process exemplified by many fruit trees such as plums, peaches, apples, apricots, and cherries. Some mutant grapes that normally would have had separate male and female individuals also became self-fertilizing hermaphrodites. By all these means, ancient farmers, who didn't understand plant reproductive biology, still ended up with useful crops that bred true and were worth replanting, instead of initially promising mutants whose worthless progeny were consigned to oblivion.

Thus, farmers selected from among individual plants on the basis not only of perceptible qualities like size and taste, but also of invisible features like seed dispersal mechanisms, germination inhibition, and reproductive biology. As a result, different plants became selected for quite different or even opposite features. Some plants (like sunflowers) were selected for much bigger seeds, while others (like bananas) were selected for tiny or even nonexistent seeds. Lettuce was selected for luxuriant leaves at the expense of seeds or fruit; wheat and sunflowers, for seeds at the expense of leaves; and squash, for fruit at the expense of leaves. Especially instructive are cases in which a single wild plant species was variously selected for different purposes and thereby gave rise to quite different-looking crops. Beets, grown already in Babylonian times for their leaves (like the modern beet varieties called chards), were then developed for their edible roots and finally (in the 18th century) for their sugar content (sugar beets). Ancestral cabbage plants, possibly grown originally for their oily seeds, underwent even greater diversification as they became variously selected for leaves (modern cabbage and kale), stems (kohlrabi), buds (brussels sprouts), or flower shoots (cauliflower and broccoli).

So far, we have been discussing transformations of wild plants into

crops as a result of selection by farmers, consciously or unconsciously. That is, farmers initially selected seeds of certain wild plant individuals to bring into their gardens and then chose certain progeny seeds each year to grow in the next year's garden. But much of the transformation was also effected as a result of plants' selecting themselves. Darwin's phrase "natural selection" refers to certain individuals of a species surviving better, and/or reproducing more successfully, than competing individuals of the same species under natural conditions. In effect, the natural processes of differential survival and reproduction do the selecting. If the conditions change, different types of individuals may now survive or reproduce better and become "naturally selected," with the result that the population undergoes evolutionary change. A classic example is the development of industrial melanism in British moths: darker moth individuals became relatively commoner than paler individuals as the environment became dirtier during the 19th century, because dark moths resting on a dark, dirty tree were more likely than contrasting pale moths to escape the attention of predators.

Much as the Industrial Revolution changed the environment for moths, farming changed the environment for plants. A tilled, fertilized, watered, weeded garden provides growing conditions very different from those on a dry, unfertilized hillside. Many changes of plants under domestication resulted from such changes in conditions and hence in the favored types of individuals. For example, when a farmer sows seeds densely in a garden, there is intense competition among the seeds. Big seeds that can take advantage of the good conditions to grow quickly will now be favored over small seeds that were previously favored on dry, unfertilized hillsides where seeds were sparser and competition less intense. Such increased competition among plants themselves made a major contribution to larger seed size and to many other changes developing during the transformation of wild plants into ancient crops.

WHAT ACCOUNTS FOR the great differences among plants in ease of domestication, such that some species were domesticated long ago and others not until the Middle Ages, whereas still other wild plants have proved immune to all our activities? We can deduce many of the answers by examining the well-established sequence in which various crops developed in Southwest Asia's Fertile Crescent.

It turns out that the earliest Fertile Crescent crops, such as the wheat

and barley and peas domesticated around 10,000 years ago, arose from wild ancestors offering many advantages. They were already edible and gave high yields in the wild. They were easily grown, merely by being sown or planted. They grew quickly and could be harvested within a few months of sowing, a big advantage for incipient farmers still on the borderline between nomadic hunters and settled villagers. They could be readily stored, unlike many later crops such as strawberries and lettuce. They were mostly self-pollinating: that is, the crop varieties could pollinate themselves and pass on their own desirable genes unchanged, instead of having to hybridize with other varieties less useful to humans. Finally, their wild ancestors required very little genetic change to be converted into crops—for instance, in wheat, just the mutations for nonshattering stalks and uniform quick germination.

A next stage of crop development included the first fruit and nut trees, domesticated around 4000 B.C. They comprised olives, figs, dates, pomegranates, and grapes. Compared with cereals and legumes, they had the drawback of not starting to yield food until at least three years after planting, and not reaching full production until after as much as a decade. Thus, growing these crops was possible only for people already fully committed to the settled village life. However, these early fruit and nut trees were still the easiest such crops to cultivate. Unlike later tree domesticates, they could be grown directly by being planted as cuttings or even seeds. Cuttings have the advantage that, once ancient farmers had found or developed a productive tree, they could be sure that all its descendants would remain identical to it.

A third stage involved fruit trees that proved much harder to cultivate, including apples, pears, plums, and cherries. These trees cannot be grown from cuttings. It's also a waste of effort to grow them from seed, since the offspring even of an outstanding individual tree of those species are highly variable and mostly yield worthless fruit. Instead, those trees must be grown by the difficult technique of grafting, developed in China long after the beginnings of agriculture. Not only is grafting hard work even once you know the principle, but the principle itself could have been discovered only through conscious experimentation. The invention of grafting was hardly just a matter of some nomad relieving herself at a latrine and returning later to be pleasantly surprised by the resulting crop of fine fruit.

Many of these late-stage fruit trees posed a further problem in that their wild progenitors were the opposite of self-pollinating. They had to be

cross-pollinated by another plant belonging to a genetically different variety of their species. Hence early farmers either had to find mutant trees not requiring cross-pollination, or had consciously to plant genetically different varieties or else male and female individuals nearby in the same orchard. All those problems delayed the domestication of apples, pears, plums, and cherries until around classical times. At about the same time, though, another group of late domesticates arose with much less effort, as wild plants that established themselves initially as weeds in fields of intentionally cultivated crops. Crops starting out as weeds included rye and oats, turnips and radishes, beets and leeks, and lettuce.

ALTHOUGH THE DETAILED sequence that I've just described applies to the Fertile Crescent, partly similar sequences also appeared elsewhere in the world. In particular, the Fertile Crescent's wheat and barley exemplify the class of crops termed cereals or grains (members of the grass family), while Fertile Crescent peas and lentils exemplify pulses (members of the legume family, which includes beans). Cereal crops have the virtues of being fast growing, high in carbohydrates, and yielding up to a ton of edible food per hectare cultivated. As a result, cereals today account for over half of all calories consumed by humans and include five of the modern world's 12 leading crops (wheat, corn, rice, barley, and sorghum). Many cereal crops are low in protein, but that deficit is made up by pulses, which are often 25 percent protein (38 percent in the case of soybeans). Cereals and pulses together thus provide many of the ingredients of a balanced diet.

As Table 7.1 (next page) summarizes, the domestication of local cereal/pulse combinations launched food production in many areas. The most familiar examples are the combination of wheat and barley with peas and lentils in the Fertile Crescent, the combination of corn with several bean species in Mesoamerica, and the combination of rice and millers with soybeans and other beans in China. Less well known are Africa's combination of sorghum, African rice, and pearl millet with cowpeas and groundnuts, and the Andes' combination of the noncereal grain quinoa with several bean species.

Table 7.1 also shows that the Fertile Crescent's early domestication of flax for fiber was paralleled elsewhere. Hemp, four cotton species, yucca, and agave variously furnished fiber for rope and woven clothing in China,

TABLE 7.1. Examples of Early Major Crop Types around the Ancient World

Area	Crop Type	
	Cereals, Other Grasses	Pulses
Fertile Crescent	emmer wheat, einkorn wheat, barley	pea, lentil, chickpea
China	foxtail millet, broomcorn millet, rice	soybean, adzuki bean, mung bean
Mesoamerica	corn	common bean, tepary bean, scarlet runner bean
Andes, Amazonia	quinoa, [corn]	lima bean, common bean, peanut
West Africa and Sahel	sorghum, pearl millet, African rice	cowpea, groundnut
India	[wheat, barley, rice, sorghum, millets]	hyacinth bean, black gram, green gram
Ethiopia	teff, finger millet, [wheat, barley]	[pea, lentil]
Eastern United States	maygrass, little barley, knotweed,	—
New Guinea	goosefoot sugar cane	—

Mesoamerica, India, Ethiopia, sub-Saharan Africa, and South America, supplemented in several of those areas by wool from domestic animals. Of the centers of early food production, only the eastern United States and New Guinea remained without a fiber crop.

Alongside these parallels, there were also some major differences in food production systems around the world. One is that agriculture in much of the Old World came to involve broadcast seeding and monoculture fields, and eventually plowing. That is, seeds were sown by being

Crop Type		
Fiber	Roots, Tubers	Melons
flax	—	muskmelon
hemp	—	[muskmelon]
cotton (<i>G. hirsutum</i>), yucca, agave	jicama	squashes (<i>C. pepo</i> , etc.)
cotton (<i>G. barbadense</i>)	manioc, sweet potato, potato, oca	squashes (<i>C. maxima</i> , etc.)
cotton <i>G. herbaceum</i>)	African yams	watermelon, bottle gourd
cotton (<i>G. arboreum</i>), flax	—	cucumber
[flax]	—	—
—	Jerusalem artichoke	squash (<i>C. pepo</i>)
—	yams, taro	—

The table gives major crops, of five crop classes, from early agricultural sites in various parts of the world. Square brackets enclose names of crops first domesticated elsewhere; names not enclosed in brackets refer to local domesticates. Omitted are crops that arrived or became important only later, such as bananas in Africa, corn and beans in the eastern United States, and sweet potato in New Guinea. Cottons are four species of the genus *Gossypium*, each species being native to a particular part of the world; squashes are five species of the genus *Cucurbita*. Note that cereals, pulses, and fiber crops launched agriculture in most areas, but that root and tuber crops and melons were of early importance in only some areas.

thrown in handfuls, resulting in a whole field devoted to a single crop. Once cows, horses, and other large mammals were domesticated, they were hitched to plows, and fields were tilled by animal power. In the New World, however, no animal was ever domesticated that could be hitched to a plow. Instead, fields were always tilled by hand-held sticks or hoes, and seeds were planted individually by hand and not scattered as whole handfuls. Most New World fields thus came to be mixed gardens of many crops planted together, rather than monoculture.

Another major difference among agricultural systems involved the main sources of calories and carbohydrates. As we have seen, these were cereals in many areas. In other areas, though, that role of cereals was taken over or shared by roots and tubers, which were of negligible importance in the ancient Fertile Crescent and China. Manioc (alias cassava) and sweet potato became staples in tropical South America, potato and oca in the Andes, African yams in Africa, and Indo-Pacific yams and taro in Southeast Asia and New Guinea. Tree crops, notably bananas and breadfruit, also furnished carbohydrate-rich staples in Southeast Asia and New Guinea.

THUS, BY ROMAN times, almost all of today's leading crops were being cultivated somewhere in the world. Just as we shall see for domestic animals too (Chapter 9), ancient hunter-gatherers were intimately familiar with local wild plants, and ancient farmers evidently discovered and domesticated almost all of those worth domesticating. Of course, medieval monks did begin to cultivate strawberries and raspberries, and modern plant breeders are still improving ancient crops and have added new minor crops, notably some berries (like blueberries, cranberries, and kiwifruit) and nuts (macadamias, pecans, and cashews). But these few modern additions have remained of modest importance compared with ancient staples like wheat, corn, and rice.

Still, our list of triumphs lacks many wild plants that, despite their value as food, we never succeeded in domesticating. Notable among these failures of ours are oak trees, whose acorns were a staple food of Native Americans in California and the eastern United States as well as a fallback food for European peasants in famine times of crop failure. Acorns are nutritionally valuable, being rich in starch and oil. Like many otherwise edible wild foods, most acorns do contain bitter tannins, but acorn lovers

learned to deal with tannins in the same way that they dealt with bitter chemicals in almonds and other wild plants: either by grinding and leaching the acorns to remove the tannins, or by harvesting acorns from the occasional mutant individual oak tree low in tannins.

Why have we failed to domesticate such a prized food source as acorns? Why did we take so long to domesticate strawberries and raspberries? What is it about those plants that kept their domestication beyond the reach of ancient farmers capable of mastering such difficult techniques as grafting?

It turns out that oak trees have three strikes against them. First, their slow growth would exhaust the patience of most farmers. Sown wheat yields a crop within a few months; a planted almond grows into a nut-bearing tree in three or four years; but a planted acorn may not become productive for a decade or more. Second, oak trees evolved to make nuts of a size and taste suitable for squirrels, which we've all seen burying, digging up, and eating acorns. Oaks grow from the occasional acorn that a squirrel forgets to dig up. With billions of squirrels each spreading hundreds of acorns every year to virtually any spot suitable for oak trees to grow, we humans didn't stand a chance of selecting oaks for the acorns that *we* wanted. Those same problems of slow growth and fast squirrels probably also explain why beech and hickory trees, heavily exploited as wild trees for their nuts by Europeans and Native Americans, respectively, were also not domesticated.

Finally, perhaps the most important difference between almonds and acorns is that bitterness is controlled by a single dominant gene in almonds but appears to be controlled by many genes in oaks. If ancient farmers planted almonds or acorns from the occasional nonbitter mutant tree, the laws of genetics dictate that half of the nuts from the resulting tree growing up would also be nonbitter in the case of almonds, but almost all would still be bitter in the case of oaks. That alone would kill the enthusiasm of any would-be acorn farmer who had defeated the squirrels and remained patient.

As for strawberries and raspberries, we had similar trouble competing with thrushes and other berry-loving birds. Yes, the Romans did tend wild strawberries in their gardens. But with billions of European thrushes defecating wild strawberry seeds in every possible place (including Roman gardens), strawberries remained the little berries that thrushes wanted, not the big berries that humans wanted. Only with the recent development of

protective nets and greenhouses were we finally able to defeat the thrushes, and to redesign strawberries and raspberries according to our own standards.

WE'VE THUS SEEN that the difference between gigantic supermarket strawberries and tiny wild ones is just one example of the various features distinguishing cultivated plants from their wild ancestors. Those differences arose initially from natural variation among the wild plants themselves. Some of it, such as the variation in berry size or in nut bitterness, would have been readily noticed by ancient farmers. Other variation, such as that in seed dispersal mechanisms or seed dormancy, would have gone unrecognized by humans before the rise of modern botany. But whether or not the selection of wild edible plants by ancient hikers relied on conscious or unconscious criteria, the resulting evolution of wild plants into crops was at first an unconscious process. It followed inevitably from our selecting among wild plant individuals, and from competition among plant individuals in gardens favoring individuals different from those favored in the wild.

That's why Darwin, in his great book *On the Origin of Species*, didn't start with an account of natural selection. His first chapter is instead a lengthy account of how our domesticated plants and animals arose through artificial selection by humans. Rather than discussing the Galápagos Island birds that we usually associate with him, Darwin began by discussing—how farmers develop varieties of gooseberries! He wrote, "I have seen great surprise expressed in horticultural works at the wonderful skill of gardeners, in having produced such splendid results from such poor materials; but the art has been simple, and as far as the final result is concerned, has been followed almost unconsciously. It has consisted in always cultivating the best-known variety, sowing its seeds, and, when a slightly better variety chanced to appear, selecting it, and so onwards." Those principles of crop development by artificial selection still serve as our most understandable model of the origin of species by natural selection.

APPLES OR INDIANS

WE HAVE JUST SEEN HOW PEOPLES OF SOME REGIONS began to cultivate wild plant species, a step with moment unforeseen consequences for their lifestyle and their descendants' place in history. Let us now return to our questions: Why did agriculture not arise independently in some fertile and highly suitable areas, such as California, Europe, temperate Australia, and subequatorial Africa? Why among the areas where agriculture did arise independently, did it develop much earlier in some than in others?

Two contrasting explanations suggest themselves: problems with local people, or problems with the locally available wild plants. On one hand, perhaps almost any well-watered temperate or tropical area the globe offers enough species of wild plants suitable for domestication. In that case, the explanation for agriculture's failure to develop in some of those areas would lie with cultural characteristics of their peoples. On the other hand, perhaps at least some humans in any large area of the globe would have been receptive to the experimentation that led to domestication. Only the lack of suitable wild plants might then explain why for production did not evolve in some areas.

As we shall see in the next chapter, the corresponding problem of domestication of big wild mammals proves easier to solve, because the